MAINTAINING AND RESTORING SPECIES DIVERSITY IN LONGLEAF PINE GROUNDCOVER: EFFECTS OF FIRE REGIMES AND SEED/SEEDLING INTRODUCTIONS

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INTRODUCTION

Longleaf pine savannas and woodlands are famous for high levels of species richness in the groundcover vegetation (Peet and Allard 1993). Maintaining this diversity, and restoring it to degraded savannas, is an important goal of ecological restoration in the southeastern USA. Two techniques for accomplishing these objectives are prescribed burning and seed/seedling introductions (Luken 1990). In fact, a combination of these methods may be necessary, since fire regime may influence successful establishment of reintroduced species.

In this paper, we summarize results to date of three long-term studies, each of which deals with effects of fire regimes on longleaf pine groundcover vegetation. In addition, one of the studies also includes seed/seedling introduction treatments, thereby allowing testing of effects of fire regimes on establishment of new species.

TIGER CORNER STUDY

The Tiger Corner study is a long-term study of the effects of frequency of burning, ongoing since 1959. Study plots are located along Tiger Corner Road in the Francis Marion National Forest, south of Jamestown, SC. The habitat is wet savanna or flatwoods. Canopy dominants include longleaf, loblolly, and pond pines. The study employs a randomized block design, with four replicates of five frequencies of fire: fire return intervals from 1-4 yrs plus unburned. All plots, except the unburned ones, were sampled at the end of the first growing season after fire, during 1992-1993. Sampling at the end of the first growing season after burning eliminated confounding between frequency of burn and time since burn, a problem in most prior studies. In each plot, all standing live biomass was harvested from eight circular 0.25 m^2 subplots. To control for confounding due to microtopography/drainage, subplots were randomly located within a narrow range of elevations common to all plots.

Results of this study indicate clear effects of fire frequency on species richness and composition of groundcover vegetation. Species richness decreases linearly with increases in between fire intervals. At the scale of 0.25 m^2, a change from annual to quadrennial burning resulted in an approximately 50% loss of species. A CANOCO (see ter Braak 1987) ordination indicated that increasing interval between fires was associated with a significant (eigenvalue = 0.24, variance explained = 14.6%, $P < .05$) shift in groundcover species composition. This shift was due to increases in the importance of woody sprouts and decreases in herbaceous plants in the less frequently burned plots. Ordinations run separately for woody and herbaceous plants failed to indicate a significant effect of frequency of burning, suggesting that, within these broadly defined groups, species are similar with respect to fire tolerance.

In general, our results are consistent with previous studies which have emphasized the importance of frequent fire for maintaining species rich groundcover in pine savannas (Peet et al. 1983, Waldrop et al. 1992, Mehlman 1992). In addition, we were able to demonstrate an important effect of fire frequency (i.e., history of frequent burning) independent of the effect of time since last burn.

ST. MARKS STUDY

This long-term study is ongoing since 1980. It includes two factors: (1) habitat (the blocking factor), and (2) season of burn. Habitats are sandhill and flatwoods. Within each habitat, eight season of burn treatments are randomly assigned to 2-5 ha plots. Treatments are replicated twice within habitats, for a total of 16 plots per habitat (block). The eight season of burn treatments are spaced at roughly six week intervals throughout the year. A variety of different kinds of data have been collected on groundcover vegetation in these plots, including data on compositional changes over time in standing biomass and one-time (1988-1989) surveys of species frequencies in 0.25 m^2 subplots (see also Streng et al. 1993).

In contrast to the Tiger Corner Study, the St. Marks study has not demonstrated obvious and consistent effects of the experimental factor on groundcover composition. CANOCO ordinations of biomass compositional changes have been largely non-significant (P's > 0.20), except in one case (sandhill biomass compositional changes between 1988 and 1994) where season of burn explained a small, but statistically significant percentage (6%) of the variation in the species data. Repeated measures ANOVAs also have not yet indicated a significant effect of season of burn on changes over time in species richness of the biomass (F's < 1.0; P's > 0.10; df=7,8; for the two habitats).

These results do not necessarily mean that season of burn is unimportant for longleaf pine groundcover vegetation. Previous studies have demonstrated significant effects of this factor on tree mortality patterns (Glitzenstein et al. 1995) and on sexual and clonal reproduction (Platt et al. 1988, Streng et al. 1993, Brewer and Platt 1994a,b). Our results do indicate, however, that effects of season of burn are variable and long-term trends are slow to develop. This is because (a) most groundcover species seem able to survive and resprout after fires regardless of when they occur, and (b) establishment of new seedlings is limited by competition and frequent fire. Thus long-term changes associated with fire effects on sexual reproduction may be very slow to develop.

WAMBAW STUDY

This final experimental study, also located in the Francis Marion National Forest, has been ongoing for five years. Like the other two studies, it is a complete randomized block experiment. The blocks are located in three longleaf pine-dominated habitats differing in drainage and surface soils (these will be referred to henceforth as the "wet", "mesic" and "dry" sites). Within each block there are three replicates of seven burning treatments: (1) winter burns every six years, (2), winter burns every 4 yrs, (3) winter burns every 2 yrs, (4) summer burns every 4 yrs, (5) summer burns every 2 yrs, (6) summer burns on average every 4 yrs, but with random between fire intervals determined by sampling from a Poisson distribution, (7) summer burns every 2 yrs; between fire intervals selected as in #6. Because of the large number of plots, fire treatments and vegetation censuses are staggered, with one set of seven plots at each habitat initiated in each of three successive years (1993-1995).

Several types of data are collected on groundcover vegetation composition in these plots. These include data on rarer species collected from variable area transects (VATs) as well as data on all species collected from six permanently located 1.5 m x 2.0 m subplots. In each plot, three randomly selected 1.5 m x 2.0 m subplots also serve as introduction sites for experimental seed additions. Seeds used in this part of the experiment are mostly machine harvested (Woodward Flail-Vac) from a variety of high quality sites within and outside of the Francis Marion National Forest. Sites are selected which contain at least one common groundcover species not currently present in the fire study plots. In addition to adding seeds, there are also two types of seedling addition plots: (1) 3 1.5 m x 4.0 m subplots per main plot containing planted grass seedlings of three species [southern wiregrass (*Aristida beyrichiana*), toothache grass (*Ctenium aromaticum*), and Indiangrass (*Sorghastrum nutans*)], and (2) subplots containing seedlings of *Parnassia caroliniana*, a rare forb (see Glitzenstein et al., this volume, for details on the *Parnassia* subplots).

To date, important results of this experiment include the following:

1) Effects of the seed introduction treatments were highly site specific. CANOCO ordinations (Before-After-Control-Impact design, in which the non-seed addition subplots represented the controls) indicated significant (eigenvalues = P < .05) effects of seed additions at the mesic and wet sites, but not at the dry site. These significant effects were due largely to wiregrass (*Aristida beyrichiana*; see Peet 1993). This species, a dominant groundcover plant throughout much of the range of longleaf pine (Peet 1993), does not presently occur in the Francis Marion National Forest, but did occur at two of the donor sites (Webb Center, Hampton County, SC; Tillman Preserve, Jasper County, SC). Following seed additions, wiregrass seedlings were present in a large majority of introduction subplots at the mesic site (32 of 39 subplots thus far recensused = 82%), a smaller percentage of subplots at the wet site (21/33 = 64%) and only a few subplots at the dry site (6/36 = 16.7%). These percentages are for seedlings which had not yet experienced a fire. Following fires, most of the subplots at the mesic site into which we had introduced wiregrass were still inhabited by seedlings of this species (14/16 = 87.5%). Comparable percentages at the wet and dry sites are 69% (9/13) and 0.0% (0/2), respectively. Thus, it appears that wiregrass seedlings are well established at the mesic and wet sites, but not at the dry site.

If wiregrass is excluded from the ordination analyses, there is no longer a significant effect of seed introductions on groundcover composition at the wet site ($P > 0.20$). However, the mesic site CANOCO is still marginally significant (P approximately 0.10). This was apparently due primarily to sparse establishment of several species not previously present at this site, including *Silphium compositum*, *Chrysopsis gossypina*, and *Helianthus radula*. Interestingly, two of these species already occur at the dry site, but the seed additions did not enhance these existing populations.

The primary conclusion from these results is that introduction via seed is difficult, except for wiregrass. This result is consistent with theory as well as results of introduction studies from other regions. For example, Tilman (1994) suggests that dominant bunchgrasses are typically superior competitors to forbs and grasses which spread clonally. Furthermore, he (Tilman 1997) found that, except for heavy-seeded legumes and some grasses, seed additions were generally ineffective in oak savanna and old field plots in Minnesota.

2) Three years after outplanting, survivorship of outplanted toothache grass and wiregrass clumps exceeds 70% except at the dry site, where toothache grass survival has now fallen to under 50%. Low survival of toothache grass at this site is not unexpected, since this grass is normally limited to wet savannas. More interestingly, wiregrass survival now exceeds toothache grass survival at all sites, even those sites where toothache grass might be expected to have the advantage. Early indications are that these differences are due to two attributes; first, wiregrass has superior survival during longer periods without fire; and second, wiregrass is more resistant than toothache grass to particularly intense fires. Indiangrass plugs have not been in the field as long as the other two species, but short-term results (1 growing season) suggest that this grass also can be successfully outplanted into frequently burned groundcover with little or no additional site preparation.

Data on wiregrass tiller growth were collected for the 1996 growing season. When corrected for effects of plant size, these data demonstrated statistically significant or almost significant positive relationships between frequency of burning and tiller growth for the dry and wet sites (r^2's= 0.55,0.37; P's=.05,.14; df=1,5). However, at the mesic site there was no effect of fire frequency on wiregrass tiller growth (r^2= 0.00, $P > 0.50$, df=1,5). A possible explanation is that groundcover at the wet and dry sites is shrub-dominated, whereas at the mesic site grasses are the dominant groundcover species. At the two shrub-dominated sites periods of fire exclusion are accompanied by rapid increases in competition as woody sprouts increase in size, resulting in suppression of wiregrass tiller growth. At the grass-dominated mesic site, periods of fire exclusion apparently do not produce similarly rapid increases in competition intensity.

3) Though all the data are not yet analyzed, results to date indicate interesting differences among species in response to fire exclusion or variable burning intervals. For example, at the dry site, certain species (e.g., *Silphium compositum*, *Tragia urens*) appear capable of persisting through periods of fire exclusion lasting up to 6 yrs, whereas other species (e.g., *Aster* spp., *Stylisma patens*) decline rapidly. In contrast to the Tiger Corner data, these data from the Wambaw Study do appear to indicate that long-term differences in fire frequencies may select among herbaceous groundcover species.

CONCLUSIONS

1. Frequent fire is necessary for maintaining characteristic composition and richness of longleaf pine groundcover. As found also by Abrahamson and Abrahamson (1996), declines in species richness due to fire exclusion or reduced frequency of fire are not reversed by single fires.

2. Season of fire is likely important for sexual reproduction of certain groundcover species (Streng et al. 1993); however, effects of this factor on groundcover composition as a whole may be very slow to develop.

3. Introducing groundcover species from seed into undisturbed vegetation appears to be a slow process, except in the case of highly competitive species such as wiregrass. However, outplanting seedlings is an efficient method for starting or enhancing populations of groundcover plants, assuming that a site is frequently burned.

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